Fig-Pollinator Interactions : Evolutionary Tug of War?

Prarthana Kathuria and K.N. Ganeshaiah
Department of Genetics & Plant Breeding
University of Agricultural Sciences
Gandhi Krishi Vignana Kendra Campus
Bangalore 560 065

Figs have a specialised type of inflorescence called syconium. There are 750 species of figs, each exclusively pollinated by a particular species of wasp. In return for the favour, the wasp utilises the ovaries of some of the female flowers for laying eggs. The fig and the wasp have co-evolved as partners, yet there seems to be a tussle to get maximum advantage from each other. The wasp would benefit by producing as many offspring as possible, and the tree would gain by having the syconia pollinated effectively without, yielding too many flowers as 'hatcheries'. The ovipositor length of the wasp is optimally determined to usurp maximum number of flowers at an affordable cost, leaving the remaining flowers for seed production.

The planet earth is home to over a million species of plants, animals and microorganisms. Almost all species interact with other species at some stage of their life cycle. Interactions could be facultative or obligate. Among obligate interactions there are antagonistic (e.g., host-parasitic) and mutualistic (e.g., plant-pollinator) interactions. One of the best known obligate mutualistic interactions is between figs and their pollinator wasps. The giant fig trees depend exclusively on tiny wasps for pollination and the wasps depend entirely on the figs for rearing their offspring.

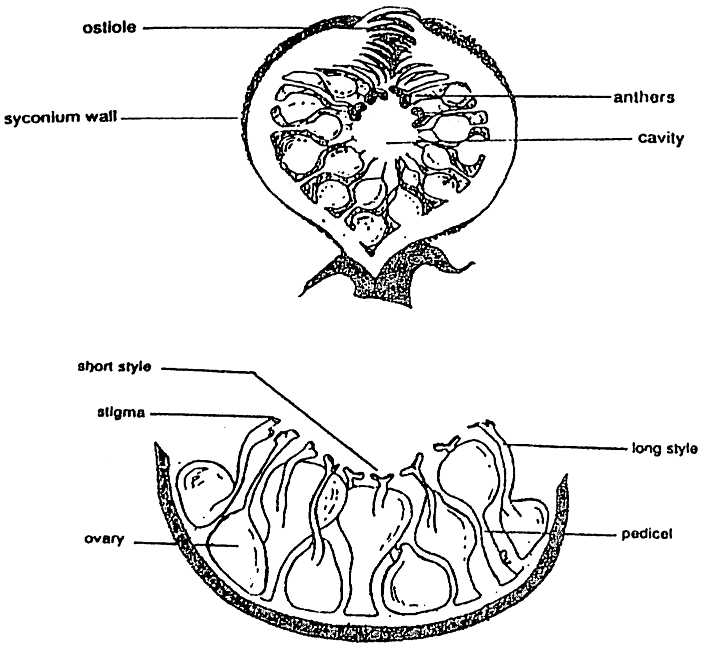

Fig. 1 : Morphology of the syconium of a typical monoecious fig species

There are about 750 species of figs found worldwide. Each species of fig (*Ficus* L., Moraceae) is exclusively pollinated by a single species of wasp. Hence, there are at least 750 species of pollinator wasps.

The Fig : The fig inflorescence is a specialised structure called a syconium (plural : syconia). The syconium is like a hollow globe with a single minute opening at the apex, the ostiole (Fig. 1). The inner side of the globe is lined with hundreds of unisexual flowers.

About half of the 750 species of figs are monoecious, the other half being gynodioecious. The inflorescences of the monoecious species contain both male and female flowers. In gynodioecious species, however, there are two kinds of trees: the male tree and the female tree. The male tree syconia contain male and female flowers, while the female tree syconia have female flowers only.

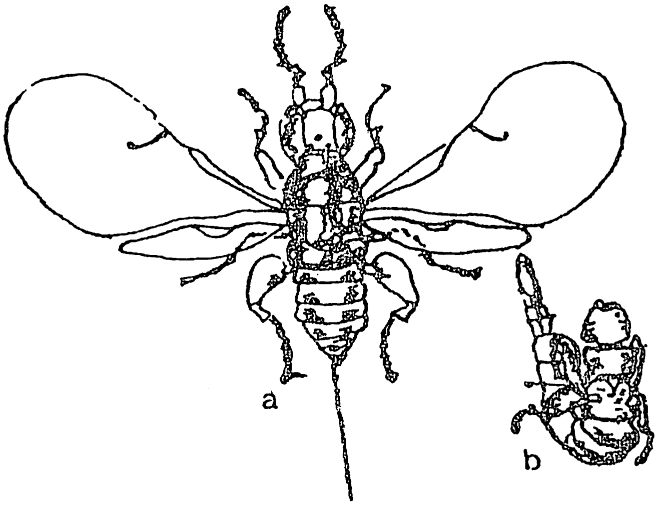

Fig. 2a : The female fig-wasp. b : The male fig-wasp

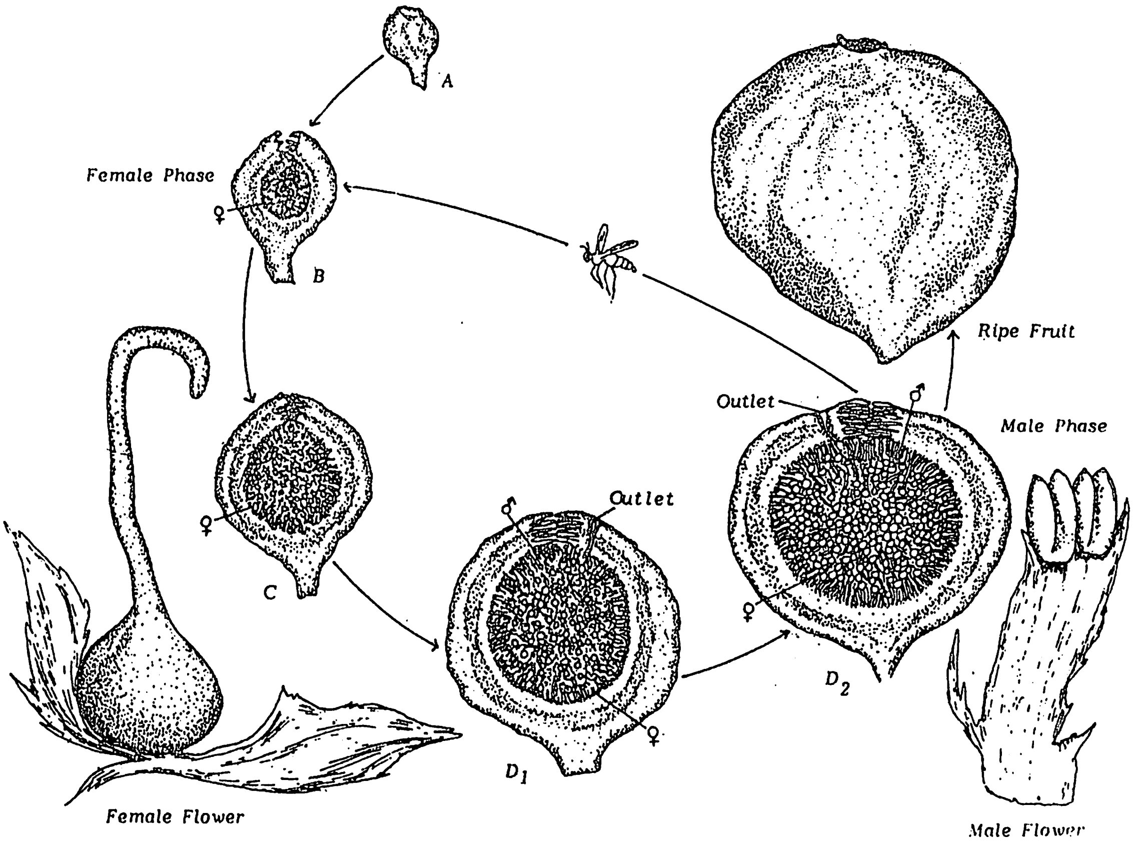

Fig. 3. The sequence of events in the fig-wasp mediated pollination of figs and the development of fig fruits.

The Wasp : The fig wasps (Agaonidae, Chalcidoidea, Hymenoptera), measure 1 to 3 mm in length. The male wasps are wingless and blind. The female wasps have very well developed wings and a long ovipositor through which they lay their eggs into the fig ovaries (Fig. 2). The female wasps also have specialised structures on the mesothoracic sternite, the pollen pockets, in which they collect pollen and carry it from one fig to another. The male wasps never leave their natal syconium; they normally die, after mating with the females, within the syconium itself. The adult life span is only two to three days.

The Fig-Wasp cycle : Hundreds to thousands of syconia start developing simultaneously on a fig tree. When the female flowers are ready to be pollinated the syconia produce specific olfactory compounds which attract the tiny female wasps. These wasps on entering the syconium through the ostiole, pollinate the flowers within, and lay eggs in some of the flowers by inserting the ovipositor through the style into the ovaries. After pollination and egg laying the mother wasp dies within the syconium.

The wasp eggs then hatch, producing larvae, which feed on the ovary tissue. The ovaries in which eggs are not laid develop into seeds while the ovaries that have been oviposited in, develop the wasp offspring. Hence both seeds and wasp larvae develop simultaneously in the syconium, in different ovaries. After 2 to 8 weeks (depending on the species) fully developed male wasps emerge from the ovaries. They locate and fertilise female wasps and start making a tunnel in the fig wall.

At this time the male flowers in the syconium are mature and ready to release pollen. The female wasps on emergence from the ovaries, collect pollen from the male flowers and escape from the fig through the tunnel constructed by the male wasps. They then fly away in search of other syconia which are ready to be pollinated, and the cycle repeats (Fig. 3).

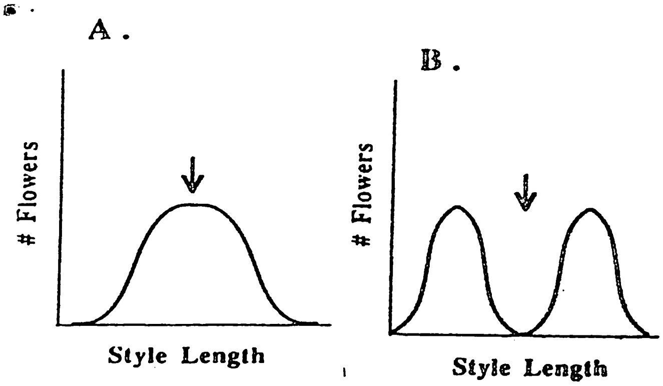

Fig. 4A. Typical normal distribution with a single mode.
B. Hypothetical bimodal distribution.

Fig-Wasp Adaptations : The figs and their pollinating wasps exhibit certain morphological and physiological adaptations that aid in the maintenance of the fig-wasp interaction suggesting a strong coevolution between them.

The high degree of protogyny seen in figs is an important adaptation to synchronise the male anthesis with the development of the pollen carrier, the wasp. The extent of protogyny is determined by the time required for the development of the next generation of wasps.

Inter-tree asynchrony in flowering and fruiting seen in figs is probably a strategy for maintaining the fig-wasp cycle since the adult wasp life span is extremely short; by flowering out of turn with other conspecifics, figs ensure a continuous supply of oviposition sites for the pollinators. Within tree synchrony observed in figs is believed to allow a stronger olfactory stimulus to the pollinator wasps, thereby attracting more pollinators to effect pollination.

Wasps too have several adaptations specific to this interaction. For instance, female wasps have flattened heads, mandibular and antennal appendages that aid in gaining access to the syconium through the ostiole. They also have specialised pollen carrying structures. The male wasps have very well developed mandibles and fore legs that are used in making the escape tunnel in the fig wall.

Conflicting Interests of the Two Partners : Though the fig-wasp cycle suggests a strong coevolution between the partners, there are several issues on which the partners can exploit each other, for instance, the regulation of number of seeds and wasps produced. The wasps increase fitness by producing as many offsprings as possible. However, the fig can increase its fitness by restricting wasp production to meet only its pollination requirement and thus increasing the number of seeds produced. Hence, there appears to be an evolutionary tug of war between the two partners over the number of flowers producing seeds and wasps.

What Prevents Wasps from Laying Eggs in All the Female Flowers? : It was believed for almost three decades that figs produce two kinds of female flowers : long styled and short styled. The ovipositor of the female wasp can reach the ovaries of only short styled female flowers and lay eggs in them. The ovipositor is too short to lay eggs in the long styled flowers, hence these develop into seeds. The proportion of short styled female flowers was thought to be half of the total flowers. This style length dimorphism hypothesis led to the belief that style lengths were bimodally distributed

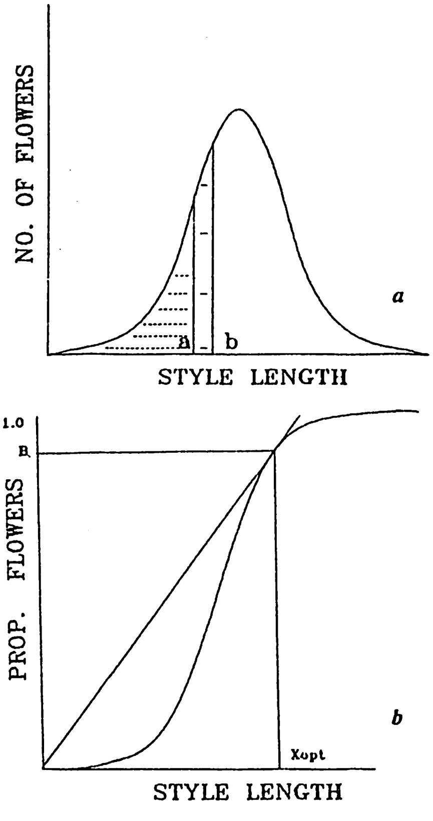

Fig. 5a. Distribution of style lengths and the proportion of flowers that can be usurped by wasps with ovipositor of length 'a' (dotted) and 'b' units (dotted + dashed).
b. Cumulative frequency distribution of style lengths that can be usurped by the wasps with increasing ovipositor lengths. The vertical line drawn to the x-axis from the tangent indicates the 'optimum ovipositor length' (Xopt). The proportion of flowers available for oviposition at Xopt length is represented by B.

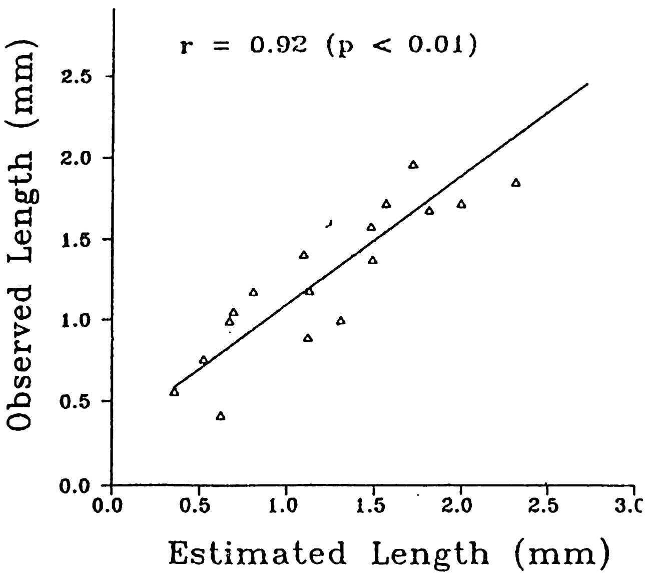

Fig. 6. Relation between estimated and observed ovipositor lengths of 18 species of wasps.

(Fig. 4B). However, some recent studies on nearly twenty-five monoecious species have revealed that there are no distinct kinds of female flowers based on style lengths, and the style length of female flowers varies continuously as a normal distribution (Fig. 4A). Thus plants do not seem to employ dimorphism in style length as a strategy to regulate the extent of flower depredation.

Recently, we have proposed an alternative mechanism for regulation of seed and wasp production (Ganeshaiah et al., 1995).

We have seen in nearly 25 species of figs that style lengths are normally distributed (Fig. 5a). Given this, a wasp with ovipositor length of 'a' units can usurp the flowers with style lengths shorter than 'a' units (the dotted area of the curve). By evolutionarily increasing its ovipositor length to 'b' units (which is longer than 'a') the wasp will be able to usurp a greater proportion of flowers (falling under the dotted and the dashed region of the curve). Similarly, the proportion of flowers usurped by wasps with different ovipositor lengths can be calculated and this cumulative curve would follow a sigmoidal shape (Fig. 5b). This curve can be considered as the benefit gained by wasps with increasing ovipositor length (y-axis). However, to increase the ovipositor length the wasps have to invest some energy in the form of production cost. This cost increases linearly with increase in ovipositor lengths hence the x-axis can be considered as increasing cost of production. As the cost increases the total benefit gained increases in the sigmoidal pattern. However, the benefit gained per unit cost (benefit to cost ratio) increases upto a certain point, reaches a maxima and then decreases. As long as the benefit gained per unit cost is increasing, natural selection will favour wasps with longer ovipositors. However, once the benefit per unit cost reaches a maximum it is no longer advantageous to possess an ovipositor longer than this, since the marginal benefit gained there after will be less than the marginal cost incurred. The maximum benefit/cost is attained at the point where tangent drawn from origin meets the cumulative distribution curve (Xopt). Hence, the optimal ovipositor length will be at the point where benefit to cost ratio is maximised. This Xopt ovipositor length is able to usurp B proportion of the flowers. Hence, a certain proportion of flowers (1-B) will by default be safeguarded for seed production.

We empirically tested the predictions of this model by comparing the observed ovipositor lengths of 18 species of wasps with the optimal ovipositor lengths estimated using this model. Clearly, the estimated ovipositor lengths (Xopt) for different species conformed with those observed. As shown in Fig. 6, the expected and observed ovipositor lengths were highly correlated ($r = 0.92$; $p < 0.01$; $Y = 0.29 + 0.79*X$; $n = 18$) suggesting that there is indeed an optimisation of the ovipositor length in the fig-wasp interaction, and could be an important mechanism for regulating seed and wasp production.

Suggested Reading

Bronstein J L 1992 Seed predators as mutualists : Ecology and evolution of the fig/pollinator interaction. In : *Insect-Plant Interactions*, IV, (ed.) Elizabeth Bernays CRC Press. Ann Arbor. p 2-43.

Galil J and D Eisikowitch 1968 On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology 49* : 259-269

Ganeshaiah K N, P Kathuria. R Uma Shanker and R Vasudeva 1995 Evolution of style length variability in figs and optimization of ovipositor lengths in their pollinator wasps : a co-evolutionary model. *J Genet 74* : 25-39.

Janzen D H 1979 How to be a fig? *Annu Rev Ecol Syst 10* : 13-15.

Kathuria P, K N Ganeshaiah, R Uma Shanker, and R Vasudeva 1995 Is there dimorphism for style lengths in monoecious figs? *Curr Sci 68* : 1047-1049.

Patel A, M Hossaert-McKey and D McKey 1993 Ficus-pollinator research in India : Past, present and future. *Curr Sci 65* : 243-252.